mature fruit, referred to this species, differ somewhat in foliage from typical L. scopulorum, and simulate Conioselinum Canadense so very closely that mature fruit is necessary to distinguish them. Collectors should carefully note whether any so-called specimens of L. scopulorum develop fruit with lateral wings. These wings are often developed so late in the maturing of the fruit that it must be fully ripe before any decision can be made.

Wabash College, Crawfordsville, Ind.

Zygomorphy and its causes. I.

CHARLES ROBERTSON.

Since reading a foot-note in Gray's Structural Botany[1] referring to the observation of Sprengel, that irregular flowers are adapted to insects, and "that strictly terminal and also vertical flowers, whether erect or suspended, are seldom irregular, while comparatively horizontal or obliquely set flowers more commonly are so," and also referring to the remark of Darwin,[2] "that he does not know of a single instance of an irregular flower which is wind-fertilized," I have often wondered what are the conditions in the insect relations of horizontal flowers which make advantageous such variations as are in the direction of irregularity. In the observation of the behavior of insects on such flowers I have found answers to some of the questions thus suggested.

Two papers on the causes of zygomorphy have recently appeared, one by Herman Vöchting[3] and the other by Frederick Delpino.[4] My observations approach the subject from a stand-point so different that it is hardly necessary to give more than references to these papers. However, it may be well, by way of introduction, to mention some of the points considered by Delpino; and I am more inclined to do this from the fact that he introduces a few terms which are convenient in characterizing irregular flowers.

Of the causes which are supposed to have operated in the production of floral irregularity Delpino recognizes three categories, viz., the instrumental and mechanical (cause stro-

---

[1] 219, note 1.

[2] Forms of Flowers, 147.

[3] Ueber Zygomorphie und deren Ursachen. Jahrb. für wissench. Botanik. Bd. XVII, H. II, 1886, 297–346. See also Bot. Zeit. 1887, 436.

[4] Zigomorfia florale e sue cause, Malpighia, Anno I, Fasc. VI, 1886, 245–262.

mentali e meccaniche), the influencing or conditional (cause influenti o condizionali), the final, functional, or biological (cause finali, funzionali, o biologiche).

Of zygomorphy four grades are distinguished. In the first grade (recentissima) the irregularity is limited to a deflection of the stamens and styles. The second (recente) and the third (inveterata) form transitions to the fourth (inveteratissima), in which there is unequal development of one or more circles with partial or total abortions of certain organs, as in the orchids. Flowers of the first two grades belong to groups in which the types are regular, those of the last two belong to zygomorphous groups.

From the point of view of final or functional causes zygomorphy is an adaptation for cross-fertilization by special insects and honey-sucking birds. Most irregular flowers are adapted to bees (melittofili). Many are adapted to hawk-moths (sfingofili) and birds (ornitofili), few to butterflies and flies. If the stamens and styles turn so as to strike the visitor on the back, the flower is *nototribe;* if they strike the under surface of the visitor, the flower is *sternotribe;* if pollen is applied to the side of the insect, the flower is *pleurotribe.*[5]

Nototribe flowers adapted to bees are most Labiatæ, Scrophulariaceæ, Bignoniaceæ, Lobeliaceæ, etc. Adapted to birds is Epiphyllum truncatum.[6] Sternotribe bee-flowers are most Papilionaceæ, Rhododendron, etc. Amaryllis formosissima is adapted to birds,[7] and Lilium longiflorum is sphingophilous. Pleurotribe flowers are adapted to bees, *e. g.*, Phaseolus, Lathyrus sylvestris and Polygala myrtifolia.[8]

Two proterandrous flowers, Teucrium Chamædrys and Ocymum Basilicum, are compared. The former is nototribe, the latter sternotribe. In the male stage in Teucrium the stamens turn down and the styles turn up; in Ocymum the stamens turn up and the style turns down. In the female stage in Teucrium the stamens turn up and the style turns down; in Ocymum the stamens turn down and the style turns up. These adaptive movements are referred to the operation of biological causes. Wind-fertilized flowers are actinomorphic, and belong to actinomorphic orders.

To the mechanical theory of De Candolle, that irregularity was caused by compression in the axils of leaves, *i. e.*,

---

[5] "Potendo darsi tre sorta d'impollinazioni, nototriba cioe, sternotriba e pleurotriba."

[6] Lobelia cardinalis and Salvia splendens are other examples. See Trelease Am. Nat. XIII. 427, and XV. 265.

[7] Tropœlum majus is commonly visited by the ruby-throated humming-bird.

[8] Perhaps better examples were described by J. E. Todd, Am. Nat. XVI. 281, Cassia Chamæcrista and Solanum rostratum.

between the leaves and the axis, it is objected that some terminal flowers are irregular, and many axillary flowers are regular.

The fifth stamen of didynamous flowers is partially or totally aborted, and is found in the plane of greatest pressure. But this stamen, if developed, would occupy the place of the style, and might defeat the contrivances for cross-fertilization, so that this abortion may also be referred to functional causes.[9] Admitting the association of the two sets of causes, which ought to be regarded as having more influence? Citing the case of Pentstemon and Jacaranda, in which the fifth stamen is even more strongly developed than the others, though not antheriferous, he says: "Behold, in this case the biological cause has triumphed over the mechanical."

In Ajuga and Teucrium the upper lip is reduced, which may be attributed to the action of mechanical causes, from being in the plane of greatest pressure, but in Salvia the upper lip is strongly developed. "Behold a new example of the prevalence of biological causes."

Since the pressure between the bracts and axis operates in a vertical direction the expansion ought to be in an horizontal direction; but the organs are most strongly developed in a vertical direction, in the plane of greatest pressure. Finally, the author concludes that, ninety times in a hundred, mechanical causes are subordinate to the functional.

To say that a flower is adapted to be cross-fertilized by certain insects seems to Delpino to be a sufficient explanation of it, but Mr. Darwin would say that it is only another way of saying that it is as we find it. If instead of "cause finali" we substitute natural selection, we shall have a known cause, and natural selection is a functional cause, since it operates only on variations which involve a functional advantage.

It is interesting, however, to observe that even teleological considerations may be sufficient objections to views which undertake to account for zygomorphy, while ignoring the selective influence of insects; for it is inconceivable that any cause, such as gravitation, should operate in such a regular way as to effect and maintain an adjustment to certain kinds of visitors. Suppose an insect lights on the stamens and styles of an horizontal flower, how can gravitation have more power to facilitate fertilization by turning these organs

[9] This abortion is attributed to natural selection by Müller (Fertilization of Flowers, 434) and Lubbock (Brit. Wild Flowers in Relation to Insects, 136).

up at the tips than to prevent it by turning them down? If it bends the styles in different directions fertilization will be more likely to occur in those flowers whose styles turn up. In this way the selective influence of insects will determine that only those flowers will be preserved whose styles are affected in a certain way by gravitation, so that the influence of gravitation will be subservient to the selective influence of insects. If, however, the action of the clinostat destroys the curvature of the styles, this character is said by Vöchting to be due to gravitation. If it fails to destroy other characters these are referred to an internal cause.

It seems to me that the principle of selection is the strength of the philosophy which undertakes to account for the origin of adaptations. There can be no doubt that different causes suggested by authors have operated to produce modifications in lateral flowers, but, as already observed, it is inconceivable that any of these causes should have had any influence in the absence of insects. On the other hand, insects can not be supposed to have produced variations, but, by determining that variations of a certain kind are advantageous, they are the cause of those modifications becoming permanent characters of the flowers, so that, after all, they may be considered to be the cause of the adaptations.

In a paper entitled "From Buttercups to Monk's-hood,"[10] Grant Allen follows a regular flower, like Ranunculus, through its transformations into an irregular form, like Aconitum. He says: "The secret of the monk's-hood depends, in the first place, upon the fact that the flowers are clustered into a spike instead of growing in a solitary isolation at the end of the stem, as in the common buttercups. Now, Mr. Herbert Spencer has pointed out that solitary terminal flowers are always radially symmetrical, and never one-sided, because the conditions are the same all around, and the visiting insects can light upon them equally from every side. But flowers which grow sideways from a spike are very apt to become bilaterally symmetrical; indeed, whenever they are not so one can always give an easy explanation of their deviation from the rule." * * "As each bee would necessarily light on the middle or lower portion of the flower, he would begin by extracting the honey from the two upper petals; but it would be rather awkward for him to turn head downward and suck the nectaries of the three bottom ones. Hence, in course of time, especially after the flower began to

[10] Pop. Sci. Monthly, XXIII, 65–68, reprinted from Knowledge.

acquire its present shape, the two top petals became specialized as nectaries, while the three lower ones gradually atrophied, since the colored sepals had practically usurped their attractive function." The views thus stated are not so fanciful as they may seem, as it is proposed to show in this paper. Instead of saying that the bee would "light on the middle or lower portion of the flower," I should say that he would light on the *middle*, and this will account for the fact that the nectaries are on the upper side. In those flowers in which the bee originally lighted on the *lower* part, the nectary is retained on the lower side and the upper nectaries abort.

Starting with the turning of a regular flower to an horizontal position, what conditions make certain modifications possible or advantageous? In the first place, an erect, regular flower attracts insects equally from all sides, and offers the expanded petals as a landing to a bee approaching from any direction. The nectaries are as conveniently reached from one side as from another. The dehiscent anthers are arranged so as to apply pollen to a bee sucking any of the nectaries. Or the nectaries and anthers are both set in the way of a bee lighting on any side. The stigmas are as likely to touch the insect coming from one side as from another.[11]

Whatever have been the causes of certain flowers assuming a more or less horizontal position, the principal advantage seems to have been a restriction of the visitors to the most diligent bees. Most of the flowers adapted to wasps, flies and butterflies, or to miscellaneous visitors, are erect and regular. The change to a lateral position has had the effect of excluding miscellaneous visitors, and has given bees the advantage, since they cling to the flowers more readily.

If small, closely crowded flowers become horizontal they may be subject to all of the conditions which are supposed to have produced irregular flowers; but they lack the selective influence of insects, and the importance of insect agency is shown from the fact that such flowers remain regular. Insects have the same relation to small, crowded, lateral flowers that they have to such flowers in flat-topped inflorescences, *i. e.*, they fertilize them by brushing over them, even pollinating many which they do not suck. They visit the inflorescence, but do not visit the single flowers in such a way as to have any particular relation to them. No one would suppose that the florets of Compositæ would become irregular by

[11] See K. F. Jordan, Die Stellung der Honigbehälter und der Befruchtungswerkzeuge in den Blumen, 1886, 54, 4).

becoming horizontal. The first condition, therefore, which is supposed to give rise to zygomorphy is that the flower must be large enough to offer some part of it as a landing to the insect.

If one wished to understand the most important characters of zygomorphic flowers he might ask this question: How did some flowers come to be sternotribe with nectaries on the upper side, and others nototribe with nectaries on the lower side? These peculiarities seem to have depended on what part of the flower originally offered a landing to the insect. Insects seem to prefer the stamens and styles as a lighting place, and to have used them as such in all cases except those in which these parts were concealed in a tube. This may be because these organs were most horizontal, or came in the way of the lower petals, and because the pollen which they bear is often the object of the visit.

According as the original characters of the flowers are supposed to favor the development of sternotribe or nototribe zygomorphy, we will consider flowers in two divisions: 1. Polypetalous (including monocotyledons), shallow gamopetalous and deep gamopetalous flowers with exserted stamens and styles. 2. Deep gamopetalous flowers with included organs.

Carlinville, Ills.

Notes on structures adapted to cross-fertilization.

AUG. F. FOERSTE.

(WITH PLATE VIII.)

Silene Pennsylvanica is proterandrous; the shorter stamens alternating with the petals maturing first, then the longer stamens. After the anthers are effete the styles separate, become hairy along one side and are ready for pollen. The cup beneath the ovary formed by the top of the anthophore forms a nectary, from which the honey may flow at times into the calyx tube below; owing to the length of this tube the flower would seem more adapted to fertilization by butterflies, but bees were most frequently observed. The crimson corolla turns bluish purple at the crown teeth as soon as the styles become effete, a sign for insect visits to cease.

Silene regia has scarlet flowers; the change of color in